

Edentulina of Madagascar (Pulmonata: Streptaxidae)

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Abstract: *Edentulina* Pfeiffer, 1856, contains some of the largest species of the diverse, carnivorous, land-snail family Streptaxidae and seems to be restricted to tropical Africa, Madagascar, and some other Indian-Ocean islands. Based on extensive collections made in 1992-1995, and on the 1994 *Faune de Madagascar* pulmonate monograph, 11 native Madagascan species of *Edentulina* Pfeiffer, 1856, can be recognized: *E. ambongoaboae* sp. nov.; *E. ambra* sp. nov.; *E. analamerae* sp. nov.; *E. ankaranae* sp. nov.; *E. antankarana* sp. nov.; *E. arenicola* (Morelet, 1860); *E. battistinii* Fischer-Piette, F. Blanc, and Salvat, 1975; *E. bemarahaе* sp. nov.; *E. bobaombiae* sp. nov.; *E. florensi* sp. nov.; *E. minor* (Morelet, 1851); *E. nitens* (Dautzenberg, 1895); and *E. rugosa* sp. nov.

Five species are synonymized under *Edentulina minor*: *E. alluandi* (Dautzenberg, 1895); *E. gaillardi* Fischer-Piette and Bedoucha, 1964; *E. intermedia* (Morelet, 1851); *E. montis* Fischer-Piette, F. Blanc, and Salvat, 1975; and *E. stumpfi* Kobelt, 1904. Three species are transferred to a new genus described in a separate paper: *Edentulina* (?) *glessi* Fischer-Piette, Blanc, Blanc, and Salvat, 1994; *E. (?) metula* (Crosse, 1881); and *E. (?) simeni* Fischer-Piette, Blanc, Blanc, and Salvat, 1994. A Seychellean species, *E. dussumieri* (Dufo, 1840), is deleted from Madagascar's faunal list.

A dichotomous key is given to the native species plus the reportedly introduced *Edentulina ovoidea* (Bruguere, 1792). Conchological descriptions are given of all native species.

Many promising regions of Madagascar remain uncollected. Further exploration should yield additional new species of *Edentulina*.

Key words: Gastropoda, Stylommatophora, land snails, taxonomy, shell variation

This paper is the first in a series on the conchological identification of Madagascar's lesser-known land-snail groups, based on extensive collections made in 1992-1995, and supplemental to the *Faune de Madagascar* monographs of Fischer-Piette *et al.* (1993, 1994).

Edentulina Pfeiffer, 1856, contains some of the largest species of the diverse, carnivorous family Streptaxidae and seems to be restricted to Africa, Madagascar, and some other Indian-Ocean islands (Zilch, 1959-1960:563). The pulmonate gastropod volume of the *Faune de Madagascar* (Fischer-Piette *et al.*, 1994) summarized knowledge of that island's *Edentulina*, listing 14 species. Among those species, three were listed as tenuous (Fischer-Piette *et al.*, 1994) and have subsequently been transferred to a new genus (Emberton and Pearce, in press): *E. (?) glessi* Fischer-Piette, Blanc, Blanc, and Salvat, 1994; *E. (?) metula* (Crosse, 1881); and *E. (?) simeni* Fischer-Piette, Blanc, Blanc, and Salvat, 1994.

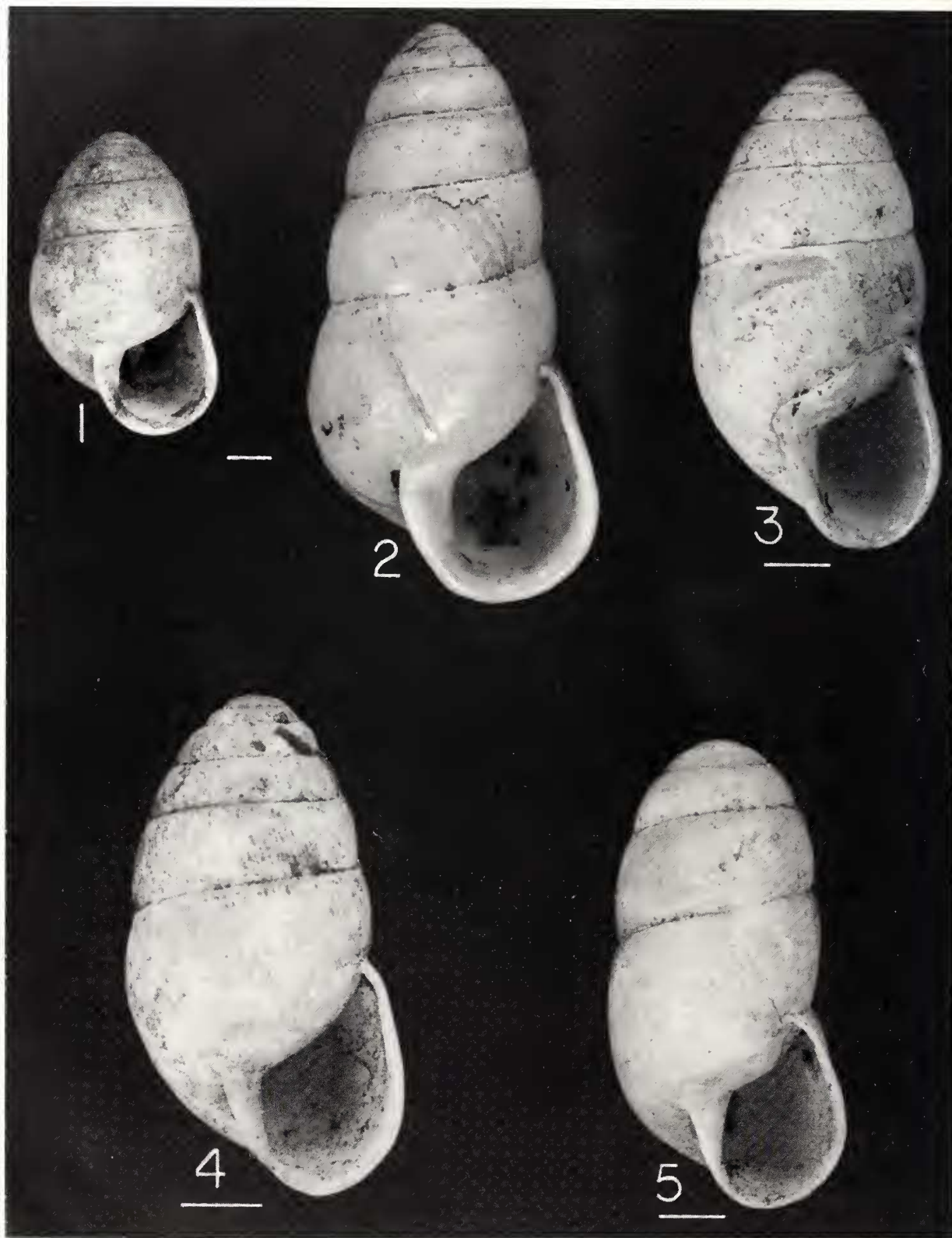
METHODS AND MATERIALS

Materials were collected in 1992-1995. Identifications and comparisons were made using Fischer-

Piette *et al.* (1994) and available collections. Authors and dates of species are given as in Richardson (1988). Whorl counts were made in apical view by the widely used method of detecting the earliest sutural notch (using incidental lighting at 40x), extrapolating that notch as a line tangent to and projecting past the suture's initial right-hand curve, counting off whorls as that line crosses successive sutures, and rounding the final fraction of a whorl—ending at the suture's end, regardless of any distortion due to apertural-lip reflection—to the nearest tenth (Emberton, 1985:fig. 1; 1989). Measurements were made using an ocular micrometer and, rarely, vernier calipers. As an index of coiling tightness, the number of whorls was divided by the natural logarithm (ln) of the shell's height. Because of Madagascar's continuing environmental crisis and the urgency of providing data to conservationists and systematists, only conchological descriptions are given here.

KEY TO SPECIES

- 1a. Subsutural spiral cord present 2
- 1b. Subsutural spiral cord absent 3
- 2a. Sculpture smooth *ovoidea*
(Fischer-Piette *et al.*, 1994:plate IV, figs. 4, 5)
- 2b. Sculpture ribbed *minor* (Figs. 1, 2, 3, 4)



Figs. 1-5. Figs. 1-4. *Edentulina minor* (Morelet, 1851): Figs. 1-2 Analamera Reserve, Fig. 3 Montagne d'Ambre National Park, Fig. 4 Namoroka Reserve. Fig. 5. *E. nitens* (Dautzenberg, 1895), Analamera Reserve. Scale bars 3 mm.

- 3a. Sculpture smooth or with only subsutural traces of ribs 4
- 3b. Sculpture weakly to strongly ribbed 6
- 4a. No preapertural deflection of body whorl *nitens* (Fig. 5)
- 4b. Upward preapertural deflection 5
- 5a. Diameter of first 1.5 whorls about 2.3 mm, no trace of subsutural ribs *ambongoaboae* (Fig. 6)
- 5b. Diameter of first 1.5 whorls 1.7-1.9 mm, trace subsutural ribs present *ankaranae* (Fig. 7)
- 6a. Ribs faint to weak 7
- 6b. Ribs strong to moderate 8
- 7a. No preapertural deflection of body whorl, coiling loose (whorls/ln height about 2.3) *ambra* (Fig. 8)
- 7b. Upward preapertural deflection, coiling tight (whorls/ln height about 2.8). *analamerae* (Fig. 12)
- 8a. Ribs and sutural crenulation very strong, embryonic whorls smooth 9
- 8b. Ribs moderate and sutural crenulation weak to moderate, embryonic whorls sculpted with riblets. 10
- 9a. Coiling tight (whorls/ln height about 2.7-3.0), shell barrel-shaped to ovate, sutures fairly deeply impressed *arenicola* (Figs. 9, 10)
- 9b. Coiling loose (whorls/ln height about 2.5), shell bullet-shaped, sutures shallowly impressed *rigosa* (Fig. 11)
- 10a. Diameter of first 1.5 whorls 1.6-1.9 mm 11
- 10b. Diameter of first 1.5 whorls 2.2-2.3. 12
- 11a. Aperture narrow (height/width 1.3) and small (0.4 shell width) *antankarana* (Fig. 13)
- 11b. Aperture broader (height/width 1.0-1.2) and larger (0.5-0.6 shell width) *bemarahae* (Figs. 15, 16, 17, 18)
- 12a. Shape fusiform-oval, never any pre-apertural duplicate peristome(s) *battistinii* (Fig. 14)
- 12b. Shape pyramidal, pre-apertural duplicate peristome(s) often present. *florensi* (Figs. 19, 20)

SYSTEMATICS

To aid users seeking only to verify a previous identification, species descriptions are ordered alphabetically as in the Abstract. Higher classification follows Vaught (1989). Type materials are placed in the United States National Museum, Washington, D.C. (USNM); the

Australian Museum, Sydney (AMS); the Muséum national d'Histoire naturelle, Paris (MNHN, which does not assign catalog numbers to types); and the Academy of Natural Sciences of Philadelphia (ANSP). Prior, working catalog numbers of the Molluscan Biodiversity Institute (MBI) are also given, because they provide reference to an ecological database available on request. MBI catalog numbers consist of station number, species reference number within that station, D (dry) or A (alcohol-preserved), and when appropriate H (holotype), P (paratype), or R (representative). As an aid to future workers, paratypes and vouchers that are illustrated and/or described herein are listed separately as "representatives," and alcohol-preserved materials for anatomical/biochemical study are listed separately (even though USNM does not assign them separate catalog numbers from dry materials of the same lots). In lot descriptions, "ad" refers to adult(s), "juv" to juveniles(s).

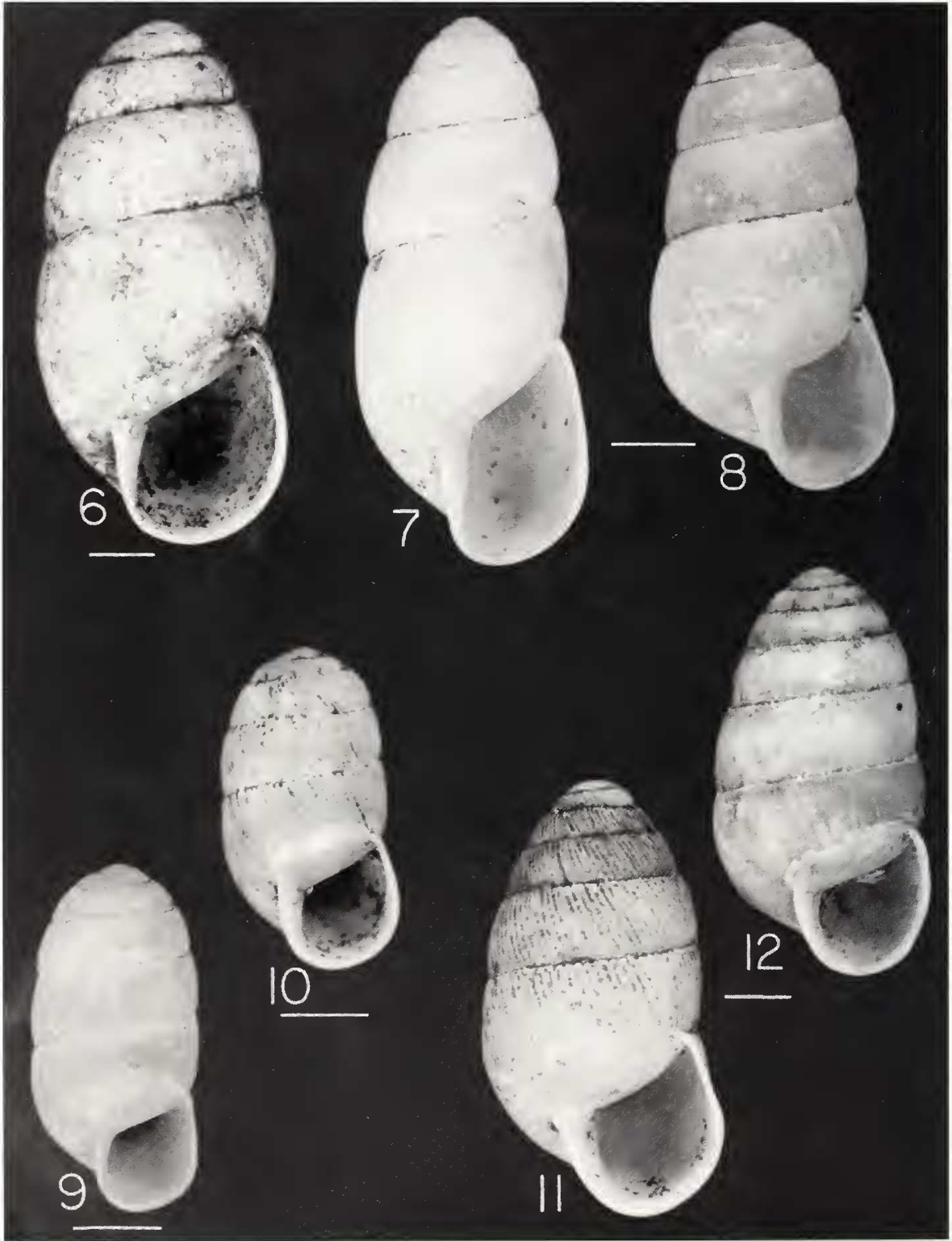
Class GASTROPODA
 Subclass PULMONATA
 Order STYLOMMATOPHORA
 Superfamily STREPTAXOIDEA
 Family STREPTAXIDAE Gray, 1860
 Genus *Edentulina* Pfeiffer, 1856

Edentulina ambongoaboae sp. nov.
 Fig. 6

HOLOTYPE. USNM 880370 (ex MBI 407.02DH, 1 ad): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo, 290 m: dry deciduous forest; 26 Aug. 1995.

DRY PARATYPES. AMS C.203515 (ex MBI 407.02DP, 1 ad): type locality. MNHN (ex MBI 405.01DP, 1 ad): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo, 320 m: baobab deciduous forest; 25 Aug. 1995. ANSP 401997 (ex MBI 405.01DP, 1 ad): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo, 320 m: baobab deciduous forest; 25 Aug. 1995. USNM 880441-880443 (ex MBI 404-407DP, 3 lots; total 5 ad): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo; Aug. 1995.

DESCRIPTION OF HOLOTYPE (a weathered shell). Shell elongate-ovoid, the aperture protruding slightly outside the ovoid profile. Height 23.8 mm, diameter 11.0 mm, whorl count 6.5, coiling tightness (whorls/ln height) 2.05. Body-whorl periphery gently rounded; suture moderately impressed, simple. Umbilicus a very narrow crevice, over half masked by reflected columellar peristome; umbilicus maximum diameter 0.5 mm. Aperture shape broad upright oval. Apertural lip reflected throughout, narrow at upper suture, then widening to a moderate reflection at the columellar insertion, with a narrow triangular, sloping shelf inside the columella. Aperture height 7.2 mm, width 6.7 mm. Preapertural deflection moderately upward, 0.1 whorl. Aperture side shape a reversed, very shallow comma.



Figs. 6-12. Fig. 6. *Edentulina ambongoaboae* sp. nov. holotype. Fig. 7. *E. ankaranae* sp. nov. holotype. Fig. 8. *Edentulina ambra* sp. nov. holotype. Figs. 9-10. *E. arenicola* (Morelet, 1860): Fig. 9 southeast of Diego Suarez, Fig. 10 Cap d'Ambre. Fig. 11. *E. rugosa* sp. nov. holotype. Fig. 12. *E. analamerae* sp. nov. holotype. Scale bars 3 mm.

Embryonic whorl count 2.6; diameter of first 1.5 whorls 2.3 mm. Embryonic sculpture smooth. Post-embryonic sculpture smooth, with faint traces of growth lines.

VARIATION. All adult specimens are remarkably uniform in size and shape.

ETYMOLOGY. For Mount Ambongoabo, the sole known locality for this species.

Edentulina ambra sp. nov.

Fig. 8

HOLOTYPE. USNM 880371 (ex MBI 191.01DH, 1 ad): 12°35'S, 49°9'E: Madagascar: Montagne d'Ambre National Park, 1260 m: rainforest; 11 July 1995.

DRY PARATYPES. AMS C.203516 (ex MBI 193.03DP, 1 juv): 12°34'S, 49°9'E: Madagascar: Montagne d'Ambre National Park, 1305 m: rainforest; 12 July 1995. MNHN (ex MBI 193.03DP, 1 juv): 12°34'S, 49°9'E: Madagascar: Montagne d'Ambre National Park, 1305 m: rainforest; 12 July 1995. USNM 880444-880456 (ex MBI 169-193DP, 8 lots; total 2 ad, 20 juv): 12°S, 49°E: Madagascar: Montagne d'Ambre National Park; July 1995.

ALCOHOL PARATYPES. USNM 880446-880457 (ex MBI 172-194AP, 10 lots; total 8 ad, 30 juv): 12°S, 49°E: Madagascar: Montagne d'Ambre National Park; July 1995.

DESCRIPTION OF HOLOTYPE. Shell a tapered column with bluntly fusiform apex, aperture scarcely protruding outside the shell's tapered-columnar profile. Height 16.6 mm, diameter 8.5 mm, whorl count 6.5, coiling tightness (whorls/ln height) 2.31. Body-whorl periphery gently rounded; suture moderately impressed, weakly crenulate. Umbilicus a circular well, fairly evenly expanding; umbilicus maximum diameter 1.1 mm. Aperture shape broad oval. Apertural lip scarcely reflected at the upper suture, broadening slightly below, then widening at the columella, where it grades into a wide, triangular, inward sloping shelf. Aperture height 4.6 mm, width 4.4 mm. No preapertural deflection. Aperture side shape nearly straight, but gently arching backward. Embryonic whorl count 2.5; diameter of first 1.5 whorls 2.1 mm. Embryonic sculpture low, narrowish, moderately spaced riblets. Post-embryonic sculpture weak ribs, nearly effaced below the periphery, but stronger at the umbilicus. Coloration pale straw-yellow.

VARIATION. Some specimens have a narrower aperture, with a height/width of up to 1.5.

ETYMOLOGY. For Montagne d'Ambre National Park.

Edentulina analamerae sp. nov.

Fig. 12

HOLOTYPE. USNM 880372 (ex MBI 210.02DH, 1 ad): 12°44'S, 49°29'E: Madagascar: Analamera Reserve, 35 m: dry deciduous floodplain; 16 July 1995.

DRY PARATYPES. AMS C.203517 (ex MBI 201.02DP, 1 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 315 m: dry deciduous forest; 15 July 1995. USNM 880458 (ex MBI

201.02DP, 1 juv): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 315 m: dry deciduous forest; 15 July 1995.

DESCRIPTION OF HOLOTYPE (apex somewhat eroded). Shell fusiform-oval, aperture protruding only slightly outside the fusiform-oval profile. Height 18.8 mm, diameter 10.1 mm, whorl count 8.1, coiling tightness (whorls/ln height) 2.76. Body-whorl periphery gently rounded; body-whorl shoulder extremely narrow, sloped about 45 degrees; suture moderately impressed, weakly crenulate. Umbilicus a nearly circular, narrow well, widened by and half covered by rapid expansion in the final 0.2 whorl; umbilicus maximum diameter 1.8 mm. Aperture obliquely egg-shaped. Apertural lip reflected throughout, narrowly at the upper suture, moderately thereafter, widening at the columella, with a narrow, steeply sloping triangular shelf below the columellar peristome. Aperture height 5.0 mm, width 5.3 mm. Preapertural deflection gradually upward, 0.3 whorl. Aperture side shape nearly straight, but slightly arching backward. Embryonic whorl count 2.8; diameter of first 1.5 whorls 2.0 mm. Embryonic sculpture smooth. Post-embryonic sculpture smoothish, with low, faint ribs. Coloration beigeish white.

ETYMOLOGY. For Analamera Reserve.

Edentulina ankaranae sp. nov.

Fig. 7

HOLOTYPE. USNM 880373 (ex MBI 580.01DH, 1 ad): 12°58'S, 49°5'E: Madagascar: Ankarana Reserve, 95 m: dry deciduous forest; 26 Aug. 1995.

DRY PARATYPES. AMS C.203518-C.203522 (ex MBI 802-815DP; 5 lots; total 9 ad, 14 juv): Madagascar: Ankarana Reserve; Oct. 1994. MNHN (ex MBI 564.02DP, 1 ad): 12°55'S, 49°5'E: Madagascar: Ankarana Reserve, 95 m: dry deciduous forest; 22 Aug. 1995. ANSP 401998 (ex MBI 564.02DP, 1 ad): 12°55'S, 49°5'E: Madagascar: Ankarana Reserve, 95 m: dry deciduous forest; 22 Aug. 1995. USNM 880459-880472 (ex MBI 557-580DP, 802-815DP, 14 lots; total 23 ad, 54 juv): Madagascar: Ankarana Reserve, 90 m: dry deciduous forest; 1994, 1995.

DESCRIPTION OF HOLOTYPE. Shell fusiform, aperture protruding slightly outside the fusiform profile. Height 19.5 mm, diameter 8.0 mm, whorl count 6.4, coiling tightness (whorls/ln height) 2.15. Body-whorl periphery very gently rounded; suture mildly impressed, simple. Umbilicus a narrow well, partially masked by reflected columellar peristome; umbilicus maximum diameter 0.5 mm. Aperture shape auriculate-oval. Apertural lip thinly reflected along outer margin, funneled basally, broadly reflected along columella and broadening greatly to the columellar insertion. Aperture height 6.1 mm, width 4.3 mm. Preapertural deflection gradually, then--abruptly--moderately upward, 0.3 whorl. Aperture side shape a reversed very shallow comma, but straight and just slightly recurved below. Embryonic whorl count 2.3; diameter of first 1.5 whorls 1.9 mm. Embryonic sculpture smooth. Post-embryonic sculp-

ture smooth, with faint growth lines and subsutural traces of ribs. Coloration ivory.

VARIATION. Adult whorls range 5.9-6.9, height 13.6-22.5 mm, coiling tightness (whorls/ln height) 2.1-2.3; shell height/diameter 2.1-2.4; embryonic whorls 2.3-2.5; diameter of first 1.5 whorls 1.7-1.9 mm.

ETYMOLOGY. For Ankarana Reserve.

Edentulina antankarana sp. nov.

Fig. 13

HOLOTYPE. USNM 880374 (ex MBI 810.02DH, 1 broken ad): 12°54'S, 49°6'E: Madagascar: Ankarana Reserve, 90 m; 10 Oct. 1994.

DRY PARATYPES. AMS C.203523 (ex MBI 810.02DP, 2 juv): type locality: 12°54'S, 49°6'E: Madagascar: Ankarana Reserve, 90 m; 10 Oct. 1994. USNM 880473 (ex MBI 810.02DP, 2 juv): type locality.

DESCRIPTION OF HOLOTYPE (adult shell from which the final 0.5 whorls are broken off, leaving some traces of adult morphology). Shell fusiform-oval. Height 22.0 mm, diameter 10.8 mm, whorl count 7.8, coiling tightness (whorls/ln height) 2.54. Body-whorl periphery gently rounded; suture well impressed, faintly crenulate. Umbilicus a narrow well with tear-drop-shaped periphery, widening abruptly (judging from scars on shell). Aperture shape uncertain, but elongate. Aperture height 6.0 mm, width 4.6 mm. Preapertural deflection weakly upward, 0.2 whorl (judging from scars on shell). Embryonic whorl count 2.8; diameter of first 1.5 whorls 1.9 mm. Embryonic sculpture very faint riblets. Post-embryonic sculpture strong, low, moderately wide, irregularly spaced ribs.

ETYMOLOGY. For the tribe of people (Antankarana) living near Ankarana Reserve.

Edentulina arenicola (Morelet, 1860)

Figs. 9, 10

REPRESENTATIVES. USNM 894278 (Fig. 9, ex MBI 217.03DR, 1 ad): 12°23'S, 49°19'E: Madagascar: Montagne des Orchides, 360 m: dry deciduous forest; 20 July 1995. USNM 894279 (Fig. 10, ex MBI 400.07DR, 1 ad): 12°10'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 70 m: dry deciduous forest; 24 Aug. 1995.

OTHER DRY VOUCHERS. AMS C.203556 (ex MBI 217.03D, 1 ad): 12°23'S, 49°19'E: Madagascar: Montagne des Orchides, 360 m: dry deciduous forest; 20 July 1995. AMS C.203548 (ex MBI 401.01D, 3 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest; 24 Aug. 1995. MNHN (ex MBI 217.03D, 1 ad): 12°23'S, 49°19'E: Madagascar: Montagne des Orchides, 360 m: dry deciduous forest; 20 July 1995. MNHN (ex MBI 401.01D, 1 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest; 24 Aug. 1995. ANSP 401999 (ex MBI 217.03D, 1 ad): 12°23'S, 49°19'E: Madagascar: Montagne des Orchides, 360 m: dry deciduous for-

est; 20 July 1995. ANSP 402000 (ex MBI 401.01D, 1 ad): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest; 24 Aug. 1995. USNM 880474-880478 (ex MBI 215-219D, 4 lots; total 10 ad, 31 juv): Montagne des Orchides; 20 July 1995. USNM 880479 (ex MBI 222.02D, 10 ad, 22 juv): 12°19'S, 49°20'E: Madagascar: Montagne des Francais, 230 m: dry deciduous forest; 21 July 1995. USNM 880480 (ex MBI 401.01D, 52 ad, 103 juv): 12°11'S, 49°13'E: Madagascar: Cap d'Ambre, la Butte Bobaomby, 205 m: dry deciduous-baobab forest; 24 Aug. 1995.

ALCOHOL VOUCHER. USNM 880477 (ex MBI 218.02A, 1 juv): 12°23'S, 49°19'E: Madagascar: Montagne des Orchides, 385 m: dry deciduous forest; 20 July 1995.

DESCRIPTION. Shell barrel-shaped, with aperture not protruding to conspicuously protruding outside the shell profile. Height 9.6-13.8 mm, height/diameter 1.7-2.0, whorl count 6.3-7.5, coiling tightness (whorls/ln height) 2.7-3.0. Body-whorl periphery flattened; suture moderately impressed, with a crenulate appearance due to rib sculpture. Umbilicus initial shape ranging from a tiny, round pinhole to a narrow well with tear-drop-shaped periphery; with abrupt widening in the final 0.2 whorls, in which the body whorl masks the preceding umbilicus; umbilicus maximum diameter approximately 0.9 mm. Aperture shape squarish-ovate to very broadly auriculate. Apertural lip reflected throughout, narrow at the upper suture, broad at the columella. Aperture size ranges from fairly small and narrow (Fig. 9; one extreme, aberrant specimen--not illustrated--with an arched columella has an aperture height/width of 2.0) to large and broad (Fig. 10; aperture height/width approaching 1.0). Preapertural deflection weakly to moderately upward, <0.05 to 0.1 whorl. Aperture side shape a reversed, very shallow comma. Embryonic whorl count 1.9-2.2; diameter of first 1.5 whorls 1.2-1.5 mm. Embryonic sculpture smooth, sometimes with a faint trace of close-set spiral striae detectable at 40x magnification. Post-embryonic sculpture consisting of strong, broad ribs. Color ivory.

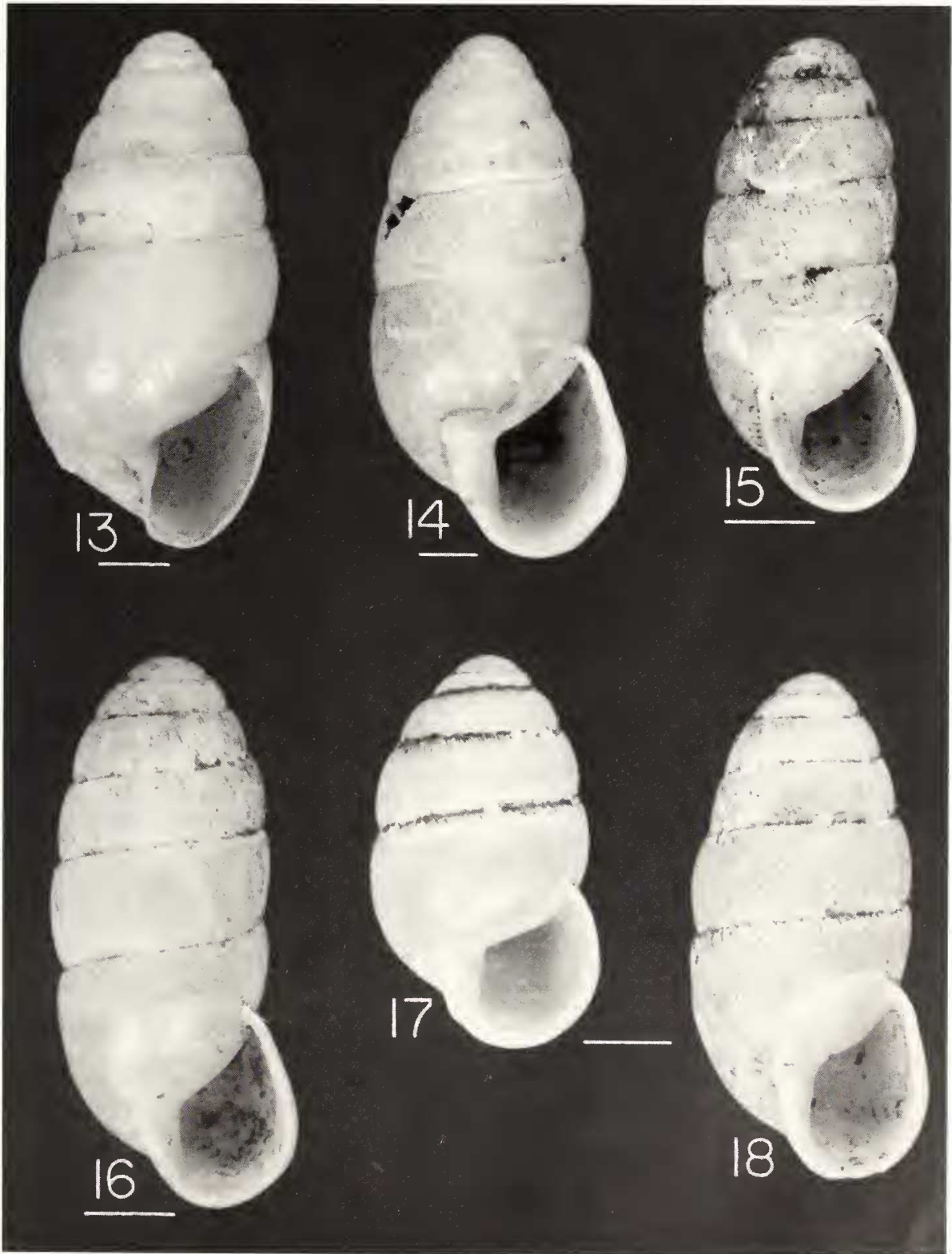
COMMENTS. Disposition of the type is unknown. The type locality is Port Leven, east of the two widely separated populations represented in Figs. 9 and 10, this paper. Previously published illustrations of *E. arenicola* are poor and misleading.

Edentulina battistinii Fischer-Piette, F. Blanc,
and Salvat, 1975

Fig. 14

REPRESENTATIVE. USNM 894280 (ex MBI 245.03DR, 1 ad): 19°8'S, 44°48'E: Madagascar: S Bemaraha Reserve: dry forest; 14 June 1995.

OTHER DRY VOUCHERS. AMS C.203524, C.203525, C.203527-C.203534 (ex MBI 245-254D, 484-494D; 10 lots; total 38 ad, 18 juv): Madagascar: Bemaraha Reserve; 1995, 1996. MNHN (ex MBI 245.03D, 1 ad): 19°8'S, 44°48'E: Madagascar: S Bemaraha Reserve: dry forest; 14 June 1995. ANSP 402001 (ex



Figs. 13-18. Fig. 13. *Edentulina antankarana* sp. nov. holotype. Fig. 14. *E. battistinii* Fischer-Piette, F. Blanc, and Salvat, 1975, Bemaraha Reserve. Figs. 15-18. *E. bemaraha* sp. nov.: Fig. 16 holotype; Figs. 15, 17, 18 paratypes. Scale bars 3 mm.

MBI 254.02D, 1 ad): 19°8'S, 44°52'E: Madagascar: S Bemaraha Reserve, 100 m: forest; 18 June 1995. USNM 880481-880492 (ex MBI 245-254D, 483-494D, 11 lots; total 40 ad, 17 juv): Madagascar: Bemaraha Reserve; 1995, 1996.

ALCOHOL VOUCHER. USNM 880492 (ex MBI 494.08A, 1 juv): 18°45'S, 44°45'E: Madagascar: N Bemaraha Reserve, 280 m: semideciduous forest; 29 June 1996.

DESCRIPTION. Shell bluntly fusiform, aperture protruding greatly outside the fusiform profile. Height 17.9-33.5 mm, height/diameter 1.8-2.5 mm, whorl count 6.8-8.8, coiling tightness (whorls/ln height) 2.4-2.5. Body-whorl periphery gently rounded, slightly flattened; body-whorl shoulder extremely narrow, sloped about 60 degrees; suture moderately impressed, very faintly crenulate. Umbilicus a moderately narrow well with tear-drop-shaped periphery, with abrupt widening in final 0.3 whorl. Aperture shape very broad auriculate-oval. Apertural lip thickly reflected, from narrow at the upper suture, through moderate and somewhat funneled at the base, to broad at the columella, with a triangular, gently sloping shelf inside the columella. Preapertural deflection gradually, then--abruptly--moderately upward, approximately 0.3 whorl. Aperture side shape a broad, distorted S, the upper curve long, the bottom curve short, both curves very shallow. Embryonic whorl count 2.9-3.0; diameter of first 1.5 whorls 2.2-2.4 mm. Embryonic sculpture faint riblets. Post-embryonic sculpture consists of strong, somewhat thin, moderately spaced ribs.

Edentulina bemaraha sp. nov.

Figs. 15, 16, 17, 18

HOLOTYPE. USNM 880375 (Fig. 16, ex MBI 247.01DH, 1 ad): 19°8'S, 44°52'E: Madagascar: S Bemaraha Reserve: riverine gallery forest; 15 June 1995.

DRY PARATYPE REPRESENTATIVES. USNM 880376 (Fig. 17, ex MBI 247.01DPR, 1 ad): type locality. USNM 880377 (Fig. 15, ex MBI 245.02DPR, 1 ad): 19°8'S, 44°48'E: Madagascar: S Bemaraha Reserve: dry forest; 14 June 1995. USNM 880378 (Fig. 18, ex MBI 254.01DPR, 1 ad): 19°2'S, 44°48'E: Madagascar: S Bemaraha Reserve: forest.

OTHER DRY PARATYPES. AMS C.203535-C.203547 (ex MBI 245-255DP, 483-495DP; 13 lots; total 24 ad, 28 juv): Madagascar: Bemaraha Reserve; 1995, 1996. MNHN (ex MBI 247.01DP, 1 ad): type locality. ANSP 402002 (ex MBI 247.01DP, 1 ad): type locality. USNM 880493-880507 (ex MBI 245-255DP, 483-495DP, 14 lots; total 25 ad, 31 juv): Bemaraha Reserve; 1995, 1996.

ALCOHOL PARATYPES. USNM 880497 (ex MBI 250.01AP, 1 juv): 19°8'S, 44°49'E: Madagascar: S Bemaraha Reserve; 16 June 1995. USNM 880503 (ex MBI 489.02AP, 2 juv): 18°41'S, 44°43'E: Madagascar: N Bemaraha Reserve, 150 m: semideciduous forest; 27 June 1996.

DESCRIPTION OF HOLOTYPE. Shell bluntly fusiform, aperture protruding greatly outside the fusiform profile. Height 18.2 mm, diameter 8.0 mm, whorl count 7.9, coiling tightness (whorls/ln height) 2.72. Body-whorl

periphery gently rounded; body-whorl shoulder very narrow, sloped about 30 degrees; suture moderately impressed, simple to weakly crenulate. Umbilicus a narrow well with tear-drop-shaped periphery, with abrupt widening in final 0.1 whorl; umbilicus maximum diameter 0.8 mm. Aperture shape broadly auriculate. Apertural lip thickly reflected, narrow at upper suture, broad at columella with sloping triangular shelf below. Aperture height 4.5 mm, width 4.3 mm. Preapertural deflection gradually, then—briefly—strongly upward, 0.5 whorl. Aperture side shape reversed very shallow comma. Embryonic whorl count 2.7; diameter of first 1.5 whorls 1.9 mm. Embryonic sculpture broad, close-set riblets. Post-embryonic sculpture strong, moderately wide, moderately spaced ribs. Coloration ivory.

VARIATION (Figs. 15-18). Adult whorls range 6.5-7.9, height 13.5-18.2, coiling tightness (whorls/ln height) 2.5-2.8; shell height/diameter 1.8-2.3; umbilicus/shell diameter 0.1-0.2; aperture height/width 1.0-1.2; aperture width/shell diameter 0.5-0.6; pre-apertural deflection 0.2-0.5 whorl; embryonic whorls 2.7-2.9; diameter of first 1.5 whorls 1.6-1.9; post-embryonic sculptural ribs vary considerably in width and density.

ETYMOLOGY. For Bemaraha Reserve.

Edentulina florensi sp. nov.

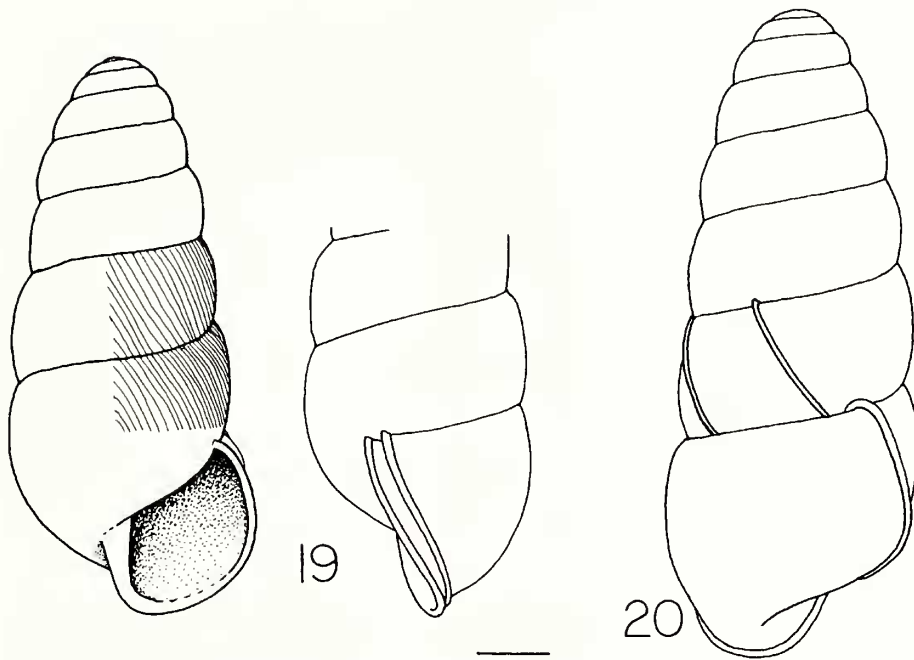
Figs. 19, 20

HOLOTYPE. USNM 880379 (Fig. 19, ex MBI 490.41DH, 1 ad): 18°45'S, 44°45'E: Madagascar: N Bemaraha Reserve, 280 m: semideciduous forest. 27-Jun-96.

DRY PARATYPE REPRESENTATIVE. USNM 880380 (Fig. 20, ex MBI 488.41DP, 1 ad): 18°47'S, 44°47'E: Madagascar: N Bemaraha Reserve, 250 m: riverine scrub. 27-Jun-96.

OTHER DRY PARATYPES. AMS C.203549-C.203554 (ex MBI 484-494DP; 6 lots; total 47 ad, 39 juv): 18°3'S, 44°31'E: Madagascar: N Bemaraha Reserve, 250 m: dry deciduous forest. 23-Jun-96. MNHN (ex MBI 494.41DP, 2 ad): 18°45'S, 44°45'E: Madagascar: N Bemaraha Reserve, 280 m: semideciduous forest. 29-Jun-96. ANSP 402003 (ex MBI 494.41DP, 2 ad): 18°45'S, 44°45'E: Madagascar: N Bemaraha Reserve, 280 m: semideciduous forest. 29-Jun-96. USNM 880508-880514 (ex MBI 484-495DP, 8 lots; total 44 ad, 42 juv): Madagascar: N Bemaraha Reserve. Jun-96.

DESCRIPTION OF HOLOTYPE. Shell tall and bluntly pyramidal. Height 22.8 mm, diameter 9.2 mm, whorl count 8.2, coiling tightness (whorls/ln height) 2.62. Body-whorl periphery gently rounded, slightly flattened; body-whorl shoulder narrow, sloped about 60 degrees; suture moderately impressed, simple to weakly crenulate. Umbilicus a narrow well with tear-drop-shaped periphery, about half covered by the reflected columellar peristome; umbilicus maximum diameter 0.8 mm. Aperture shape auriculate-oval. Apertural lip very narrowly reflected at the upper suture and to the basal area, whence it expands to a broadly triangular columellar insertion, within which is a narrow, trian-



Figs. 19-20. *Edentulina florensi* sp. nov.: Fig. 19 holotype in two views; Fig. 20 paratype. Scale bar 3 mm.

gular, steeply sloping shelf. Aperture height 5.0 mm, width 5.1 mm. Preapertural deflection gradually upward, 0.2 whorl. Aperture side shape a reversed, very shallow comma. Embryonic whorl count 2.8; diameter of first 1.5 whorls 2.2 mm. Embryonic sculpture riblets. Post-embryonic sculpture moderately strong, thin ribs, moderately spaced; a conspicuous, pre-apertural, duplicate peristome is present. Coloration ivory.

VARIATION (Figs. 19-20, in part). Presumed adult whorls range 6.7-9.2, height 15.8-29.4; shell height/diameter 1.9-3.0; coiling tightness (whorls/ln height) 2.4-2.7; one or more pre-apertural, duplicate peristomes occur in about three-fourths of presumed adults.

ETYMOLOGY. For Vincent Florens, in recognition of his outstanding contribution to the first Bemaraha expedition.

Edentulina minor (Morelet, 1851)

Figs. 1, 2, 3, 4

NEW SYNONYMS. *Edentulina alhuandi* (Dautzenberg, 1895) (Fig. 3; Fischer-Piette *et al.*, 1994:57, plate IV fig. 11). The slender shape of this variant from Montagne d'Ambre (see below) falls within the morphological range of *E. minor* from other sites such as Namoroka Reserve (see below).

Edentulina gaillardi Fischer-Piette and Bedoucha, 1964 (Fig. 4; Fischer-Piette *et al.*, 1994:57, plate IV fig. 11). A wide-apertured, strong-ribbed variant of *E. minor* from Ankarafantsika Reserve and environs (including

Ampijoroa Reserve, see below), which also occurs within *E. minor*'s range of variation within Namoroka Reserve (see below).

Edentulina intermedia (Morelet, 1851) (Fischer-Piette *et al.*, 1994:50, fig. 33). Fischer-Piette was unable to locate the holotype, so he reproduced Morelet's inadequate figure and measurements; he also commissioned numerous collections at the sole known locality (Port-Léven), but without success (Fischer-Piette and Bedoucha, 1964). Fortunately, however, Tryon (1885:83; plate 17, fig. 20) had adequately illustrated and remeasured the holotype, which falls within *E. minor*'s known range of variation.

Edentulina montis Fischer-Piette, F. Blanc, and Salvat, 1975 (Fischer-Piette *et al.*, 1994: 57, plate IV fig. 12-14). Despite its narrow umbilicus, this species seems to fall within the wide variation of *E. minor*, which occurs at the type locality of *E. montis*, Montagne des Francais (see below).

Edentulina stumppfii Kobelt, 1904 (Fischer-Piette *et al.*, 1994: 51, Fig. 34). On Nosy Be, the type locality of *E. stumppfii*, many *E. minor* were collected (see below), within whose range of variation *E. stumppfii* seems to fall.

REPRESENTATIVES. USNM 894281 (Figs. 1 and 2, ex MBI 203.03DR, 2 ad): 12°44'S, 49°30'E: Madagascar: Analamera Reserve, 285 m: bamboo-dry deciduous thicket; 16 July 1995. USNM 894282 (Fig. 3, ex MBI 184.01DR, 1 ad): 12°36'S, 49°9'E: Madagascar: Montagne d'Ambre National Park, 1165 m: rainforest; 10 July 1995. USNM

894283 (Fig. 4, ex MBI 61.03DR, 1 ad): 16°23'S, 45°18'E: Madagascar: Namoroka Reserve, 105 m: dry deciduous forest; 25 May 1995.

OTHER DRY VOUCHERS. AMS C.203514 (ex MBI 184.01D, 1 ad): 12°36'S, 49°9'E: Madagascar: Montagne d'Ambre National Park, 1165 m: rainforest; 10 July 1995. AMS C.203555 (ex MBI 83.01D, 1 ad): 16°17'S, 46°49'E: Madagascar: Ampijoroa Reserve, 95 m: hardwood deciduous forest; 3 June 1995. AMS C.203558 (ex MBI 55.03D, 2 ad): 16°23'S, 45°21'E: Madagascar: Namoroka Reserve, 110 m: dry deciduous forest; 21 May 1995. AMS C.203559 (ex MBI 487.01D, 3 ad, 4 juv): 18°S, 44°E: Madagascar: N Bemaraha Reserve; 25 June 1996. AMS C.203560 (ex MBI 805.03D, 6 ad, 8 juv): 13°1'S, 49°0'E: Madagascar: Ankarana Reserve, 50 m: 8 Oct. 1994. MNHN (ex MBI 55.03D, 2 ad): 16°23'S, 45°21'E: Madagascar: Namoroka Reserve, 110 m: dry deciduous forest; 21 May 1995. MNHN (ex MBI 83.01D, 1 ad): 16°17'S, 46°49'E: Madagascar: Ampijoroa Reserve, 95 m: hardwood deciduous forest; 3 June 1995. MNHN (ex MBI 184.01D, 1 ad): 12°36'S, 49°9'E: Madagascar: Montagne d'Ambre National Park, 1165 m: rainforest; 10 July 1995. ANSP 402004 (ex MBI 55.03D, 2 ad): 16°23'S, 45°21'E: Madagascar: Namoroka Reserve, 110 m: dry deciduous forest; 21 May 1995. ANSP 402005 (ex MBI 83.01D, 1 ad): 16°17'S, 46°49'E: Madagascar: Ampijoroa Reserve, 95 m: hardwood deciduous forest; 3 June 1995. ANSP 402006 (ex MBI 184.01D, 1 ad): 12°36'S, 49°9'E: Madagascar: Montagne d'Ambre National Park, 1165 m: rainforest; 10 July 1995. USNM 880515-880527 (ex MBI 55-74D, 13 lots; total 148 ad, 148 [no mistake] juv): Madagascar: Namoroka Reserve; May 1995. USNM 880528-880531 (ex MBI 81-84D, 4 lots; total 28 ad, 57 juv): 16°17'S, 46°49'E: Madagascar: Ampijoroa Reserve; June 1995. USNM 880532 (ex MBI 86.01D, 1 juv): 16°8'S, 47°0'E: Madagascar: Ankarafantsika Reserve, 160 m: dry deciduous forest; 5 June 1995. USNM 880533-880549 (ex MBI 118-150D, 17 lots; total 14 ad, 42 juv): 13°S, 48°E: Madagascar: Nosy Be: Lokobe Reserve; June 1995. USNM 880550 (ex MBI 168.01D, 2 ad, 1 juv): 13°34'S, 48°45'E: Madagascar: Galoko Escarpment, 225 m: hardwood-palm rainforest; 4 July 1995. USNM 880551-880560 (ex MBI 177-194D, 10 lots; total 6 ad, 19 juv): 12°S, 49°E: Madagascar: Montagne d'Ambre National Park; July 1995. USNM 880561-880575 (ex MBI 199-214D, 15 lots; total 39 ad, 102 juv): 12°S, 49°E: Madagascar: Analamera Reserve; July 1995. USNM 880576-880577 (ex MBI 217-219D, 2 lots; total 6 ad, 7 juv): 12°23'S, 49°19'E: Madagascar: Montagne des Orchides; 20 July 1995. USNM 880578-880579 (ex MBI 220-221D, 2 lots; total 1 ad, 10 juv): 12°19'S, 49°20'E: Madagascar: Montagne des Francais; 21 July 1995. USNM 880580-880591 (ex MBI 230-240D, 402-407D, 12 lots; total 25 ad, 80 juv): Madagascar: Cap d'Ambre; 1995. USNM 880592 (ex MBI 410.01D, 1 juv): 12°26'S, 49°12'E: Madagascar: W of Sakaramy, S of Diego Suarez, 470 m: dry deciduous viny forest; 26 Aug. 1995. USNM 880593-880600 (ex MBI 412-421D, 8 lots; total 10 ad, 29 juv): Madagascar: Andavakoera massif, N of Betsiaka; 1995. USNM 880601 (ex MBI 487.01D, 4 ad, 4 juv): 18°S, 44°E: Madagascar: N Bemaraha Reserve; 25 June 1996. USNM 880602 (ex MBI 548.01D, 9 juv): 13°28'S, 48°21'E: Madagascar: Nosy Komba, 622 m: cleared, former forest; 23 June 1995.

USNM 880603-880605 (ex MBI 564-572D, 805D, 3 lots; total 9 ad, 13 juv): Madagascar: Ankarana Reserve; 1994, 1995.

ALCOHOL VOUCHERS. USNM 880516-880523 (ex MBI 56-70A, 2 lots; total 2 juv): 16°S, 45°E: Madagascar: Namoroka Reserve; May 1995. USNM 880530-880531 (ex MBI 83-84A, 2 lots; total 2 juv): 16°17'S, 46°49'E: Madagascar: Ampijoroa Reserve; June 1995. USNM 880538-880549 (ex MBI 125-150A, 7 lots; total 11 juv): Madagascar: Nosy Be: Lokobe Reserve; June 1995. USNM 880567-880574 (ex MBI 206-213A, 2 lots; total 1 ad, 2 juv): 12°S, 49°E: Madagascar: Analamera Reserve; July 1995. USNM 880585 (ex MBI 239.01A, 1 ad): 12°0'S, 49°17'E: Madagascar: Cap d'Ambre, near Ambatojanahary, 40 m: dry deciduous forest; 25 July 1995. USNM 880594-880600 (ex MBI 413-421A, 3 lots; total 3 juv): 13°S, 49°E: Madagascar: Andavakoera massif, N of Betsiaka; 1995.

DESCRIPTION. Shell acute-oval to fusiform, aperture protruding moderately to greatly outside the oval-to-fusiform profile. Height 16.4-37.2 mm, height/diameter 1.6-2.0, whorl count 6.9-9.0, coiling tightness (whorls/ln height) 2.4-2.5. Body-whorl periphery rounded; body-whorl shoulder a very narrow shelf defined by a subsutural cord; suture shallowly to moderately impressed, simple to faintly undulating to faintly crenulate. Subsutural spiral cord present. Umbilicus a slit-like crevice or crease to a tear-drop-shaped well, abruptly widened by rapid expansion in final 0.2-0.4 whorl; umbilicus maximum diameter/shell diameter 0.2. Aperture shape broad auriculate-oval. Apertural lip unreflected to narrowly reflected at the upper suture, moderately and thickly relected thereafter, the columella broadened by a triangular shelf slanting inward within the aperture. Aperture width/shell diameter 0.5-0.6; apertural height/width 1.0-2.0. Preapertural deflection weakly to moderately upward, 0.1-0.2 whorl. Aperture side shape a reversed, shallow comma, but straight and slightly recurved below. Embryonic whorl count 2.6-3.1; diameter of first 1.5 whorls 1.8-2.0 mm. Embryonic sculpture smooth, sometimes with very faint traces of low riblets in the final half whorl. Post-embryonic sculpture weak to moderately strong, closely spaced ribs. Coloration ivory to yellowish beige.

Edentulina nitens (Dautzenberg, 1895)

Fig. 5

REPRESENTATIVE. USNM 894284 (ex MBI 210.04DR, 1 ad): 12°44'S, 49°29'E: Madagascar: Analamera Reserve, 35 m: dry deciduous floodplain; 16 July 1995.

DESCRIPTION OF REPRESENTATIVE (embryonic shell severely fractured and repaired during life). Shell blunt elongate-oval. Height 20.6 mm, diameter 10.4 mm, whorl count 6.7, coiling tightness (whorls/ln height) 2.21. Body-whorl periphery flattened; suture well impressed, simple. Umbilicus a narrow well, scarcely widened in final 0.1 whorl; umbilicus maximum diameter 0.8 mm. Aperture

shape broadly auriculate-oval. Apertural lip nearly unreflected at the upper suture, then narrow, widening greatly at the columella into a triangular insertion, with a narrow, steep shelf below the columella. Aperture height 6.1 mm, width 5.3 mm. No preapertural deflection. Aperture side shape a reversed, very shallow comma, but straight and just slightly recurved below. Embryonic whorl count 2.4; diameter of first 1.5 whorls 1.8 mm. Embryonic sculpture smooth. Post-embryonic sculpture smooth, with faint, very regularly spaced growth lines. Coloration ivory.

Edentulina rugosa sp. nov.

Fig. 11

HOLOTYPE. USNM 880381 (ex MBI 407.04DH, 1 ad): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo, 290 m: dry deciduous forest; 26 Aug. 1995.

DRY PARATYPES. AMS C.203561 (ex MBI 406.01DP, 1 ad): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo, 310 m: baobab deciduous forest; 25 Aug. 1995. MNHN (ex MBI 405.03DP, 1 ad): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo, 320 m: baobab deciduous forest; 25 Aug. 1995. ANSP 402007 (ex MBI 405.03DP, 1 ad): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo, 320 m: baobab deciduous forest; 25 Aug. 1995. USNM 880606-880607 (ex MBI 405-407DP, 2 lots; total 4 juv): 12°15'S, 49°15'E: Madagascar: Cap d'Ambre, Ambongoabo; Aug. 1995. USNM 880608-880609 (ex MBI 410-411DP, 2 lots; total 1 ad, 5 juv): 12°26'S, 49°12'E: Madagascar: W of Sakaramy, S of Diego Suarez; Aug. 1995.

DESCRIPTION OF HOLOTYPE. Shell fusiform-oval. Height 20.2 mm, diameter 10.7 mm, whorl count 7.4, coiling tightness (whorls/ln height) 2.46. Body-whorl periphery slightly flattened; suture mildly impressed, strongly crenulate from ribbed sculpture. Umbilicus a moderately wide well, rapidly expanded in last 0.1 whorl; umbilicus maximum diameter 1.5 mm. Aperture shape broadly auriculate. Apertural lip narrowly reflected at the upper suture, broadening to widely reflected at the columella, which continues inward as a triangular sloping shelf. Aperture height 5.8 mm, width 5.8 mm. Preapertural deflection gradually upward, 0.2 whorl. Aperture side shape a reversed, extremely shallow comma, straightened and very slightly recurved at the bottom. Embryonic whorl count 2.6. Embryonic sculpture smooth, with a hint of dense spiral lines visible at 40x magnification. Post-embryonic sculpture very strongly ribbed. Coloration light beige.

VARIATION. Adult height ranges from 16.7 to 22.8 mm.

ETYMOLOGY. For the conspicuous sculpture that is strongly wrinkled (Latin "rugosa") or ribbed.

DISCUSSION

Fischer-Piette *et al.*'s (1994) faunal list tentatively included two extra-Madagascan *Edentulina*: *E. ovoidea* (Bruguere, 1792) of East Africa and the Comores, and *E.*

dussumieri (Dufo, 1840) of the Seychelles. Neither of those species was encountered in the 1992-1995 survey. *E. ovoidea* should remain tentatively on the faunal list, because it reportedly was introduced (misguidedly) as a biological control agent to Madagascar (Fischer-Piette *et al.*, 1994:49-50). It seems safe, however, to remove *E. dussumieri*, because it has never been collected in Madagascar since Morelet's old and non-vouchered report.

Based on collections made in 1992-1995 from at or near their type localities, four species are synonymized above under *E. minor* (Morelet, 1851): *E. alluaudi* (Dautzenberg, 1895); *E. gaillardi* Fischer-Piette and Bedoucha, 1964; *E. montis* Fischer-Piette, F. Blanc, and Salvat, 1975; and *E. stumpfii* Kobelt, 1904. *E. intermedia* (Morelet, 1851) is also synonymized under *E. minor*, based on Tryon's (1885) redescription of the holotype, and based on numerous barren collections at the type locality (Fischer-Piette and Bedoucha, 1964).

Thus, of Fischer-Piette *et al.*'s (1994) list of 13 native species of Madagascan *Edentulina*, this paper deletes one, transfers three, and synonymizes five. This leaves four, all of which were collected in 1992-1995 and are described (from representatives) above. With the addition of 7 new species, also described above, Madagascar's list of *Edentulina* now totals 11 native species and, possibly, the one introduced species.

Many promising regions of Madagascar remain uncollected, so exploration should yield additional new species of *Edentulina*.

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